Sex-biased predation on moths by insectivorous bats

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Abstract. Two species of insectivorous bats, Lasiurus cinereus and L. borealis, ate significantly more male than female moths in the wild. The observed bias was likely to be a consequence of sexual dimorphism in moth flight activity associated with sexual differences in mate acquiring mechanisms. Female moths flew less than males and their activity peaks occurred at different times. The peak of male activity coincided with a peak in bat activity in the middle of the night, while female activity peaked earlier in the night when bat activity was relatively low. The results of this study are interpreted in a sexual selection framework, and the conclusions about predation risk from bats that hunt airborne prey are applicable to all nocturnally flying insects that exhibit sexual dimorphism in flight activity.

Inter-sexual differences in parental investment bias the ratio of sexually receptive females to males and generate competition among members of the sex investing less time and energy in offspring for members of the sex investing more in offspring (Trivers 1972). The sex that provides relatively little parental investment (usually males), has a much greater potential rate of reproduction than the other sex (Clutton-Brock & Vincent 1991). Because of this high reproductive potential, selection favours a tendency in males to exhibit traits (for locating, attracting or competing for females) that increase the probability of mating successfully (Krebs & Davies 1993); these traits, however, may also place males at a higher risk of predation than females (Magnhagen 1991). It is often difficult to observe predation in the wild, therefore relatively few studies have directly demonstrated higher male mortality due to predation or parasitism (e.g. Cade 1975; Burk 1982; Gwynne 1987; Sakaluk 1990; Rehfelt 1992).

Moths use a pheromone-based system for long-distance communication between the sexes. In most moth species, males follow pheromone plumes emitted by a stationary female (Greenfield 1981). Females of most moth species can fly, but flight is usually used for finding oviposition sites, escaping from predators and, in some cases, for finding food. Flight in females is sluggish and, in many species, females do not fly until they have mated and deposited some of their egg mass. In some moth species, females are flightless (Sattler 1991).

Sexual dimorphism in moth flight activity should put males at a higher risk of predation than the more sedentary females. Moths make up a large proportion of the diets of many species of insectivorous bats (Whitaker 1988), and for some bat species foraging in particular areas, moths are the main food items (e.g. Acharya & Fenton 1992). For many adult moths, it is likely that insectivorous bats are their major nocturnal predators. The importance of bats as predators of moths is apparent in that many species of moths possess echolocation (bat) detecting ‘ears’ (Fullard 1987). In this paper, I present evidence for male-biased predation on moths by insectivorous bats in the field that supports the hypothesis that searching for mates is a risky behaviour.

METHODS

The study was conducted at Pinery Provincial Park near Grand Bend, Ontario, Canada (81.83°W, 43.25°N) in June, July and August of 1992 and 1993. The park is situated on the shore of Lake Huron. The vegetation is composed mostly of oak (Quercus spp.) and plantation pine (Pinus resinosa and P. strobus). At this site, bats feed around street lights that illuminate three campground entrances and the park's main entrance. These lights are the foci of bat and insect activity (Hickey & Fenton 1990). Lasiurus cinereus and L. borealis (Vespertilionidae) are the two most common bat species at these lights, although
Figure 1. Schematic representation of sexual dimorphism in wing coupling structures found in species of moths examined in this study; f: frenulum, r: retinaculum.

Eptesicus fuscus and Myotis lucifugus also occasionally feed on insects at the lights. Lasius cinereus and L. borealis attack moths that fly around the lights (Hickey & Fenton 1990; Acharya & Fenton 1992) and the outcome of their attacks is clearly visible with the aid of a hand-held spotlight.

To determine the sex ratio of the moths eaten by the bats (to test the null hypothesis that the ratio did not deviate from unity), I examined wings culled and dropped by foraging bats. Culled wings fluttered towards the ground following a successful attack, and were caught with a hand net. I collected only wings that I could unambiguously assign to a single attack. In 1992 and 1993, wings were examined from 33 nights (146 h) and 19 nights (136.8 h) of observation, respectively. In 1992, wings were collected for only part of the night (85 ± 250.9 ± 80.2 min from sunset). In 1993, wings were collected from dusk to dawn, weather permitting (T± s=432.1 ± 94.7 min from sunset). The wings were identified to family after Cove11 (1984) and the sex recorded. In many moth families, specialized structures hold the wings together in flight, and in most species there is sexual dimorphism in these structures (Eaton 1988; Scoble 1992). In males, a spine, or frenulum, arising from the base of the hind wing attaches to a hook or flap, the retinaculum, on the underside of the forewing (Fig. 1). In females, the frenulum is usually composed of two or more spines that arise from the hind wing base. The retinaculum in females is a patch of stiff hairs or scales on the underside of the forewing (Fig. 1). I included moths from the families Noctuidae, Notodontidae, Arctiidae and Geometridae in the analysis because they were the most numerous medium-sized moths flying around the lights. Microlepidopterans were excluded because their culled wings were often damaged, and could not be accurately identified to sex. Culled wings from the gypsy moth, Lymantria dispar (Lymantriidae), were not included in the analysis because females of this species are flightless.

To determine the overall sex ratio of the community of moths flying around the lights, I set a light trap at a site a few hundred metres from where the bats were foraging. The trap was set once a week for 12 weeks (early June to late August) in 1992 and 1993. In 1993, to examine moth activity patterns across the night, I divided the nightly trapping period into three intervals: early, middle and late. The early period began at the end of Civil Twilight (sun's disk 12' below the horizon) and ended 2 h later. The late period included the 2 h before the beginning of Civil Twilight. The middle period included the period between the end of the early period and beginning of the late period, and varied according to time of season (range= 190-405 min). In 1992, traps were set only for the early and middle parts of the night. Moths caught in the trap were later identified to family and to sex. I calculated the ratio of male to female moths caught by the trap over the whole summer and determined whether the ratio differed from 1:1. Similarly, I compared the trap sex ratio with the sex ratio obtained from culled wings. Additionally, I calculated the mean density of moths per h for each sex during each period of the night, and compared patterns of activity over the night between the two sexes.

Concurrent with the insect sampling in 1993, I measured activity of bats across the night (for 12 nights). Activity was monitored with two bat detectors (Ultrasound Advice, London). One detector was tuned to 20 kHz (the frequency containing the most energy for L. cinereus) and the second detector was tuned to 40 kHz (the frequency containing the most energy for L. borealis). Echolocation calls of the two species are clearly distinguishable because of these frequency differences and differences in call length (Fenton & Bell 1981). Echolocation calls were monitored for one 10-min period at the beginning of each hour. One listener counted passes (a train of echolocation calls produced by an individual bat) and feeding buzzes (a series of echolocation calls produced at a rapid rate as a bat attacks a
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flying insect; Griffin 1958) for *L. cinereus*, and the second listener did the same thing for *L. borealis*. The same listener was always responsible for monitoring the same species. I compared the mean number of passes and buzzes per 10-min sampling interval among periods of the night and between species, and I compared patterns of activity (for passes and buzzes) over the night between the two species.

Sex ratios were compared using chi-squared analyses on raw data. I used analysis of variance (ANOVA) to compare mean moth density between periods, and bat activity between periods. Where the standard deviations were proportional to the means, ANOVA was performed on log-transformed (log x+0.01) data to correct for heteroscedasticity. Untransformed means are reported. A rejection level of 0.05 was used in all tests, and all tests were two-tailed. Statistical Analysis Systems software (SAS 1985) was used to perform the ANOVA.

**RESULTS**

In 1992 and 1993, bats caught significantly more male than female moths (1992: 4.7:1, $\chi^2=75.63$, df=1, $P<0.001$; 1993: 5.8:1, $\chi^2=66.85$, df=1, $P<0.001$; Fig. 2), and there was no significant difference between the 2 years ($\chi^2=0.57$, df=1, $P>0.1$). The data from the light trap showed a similar significant bias towards the capture of males (1992: 3:01:1, $\chi^2=133.75$, df=1, $P<0.001$; 1993: 3:04:1, $\chi^2=195.02$, df=1, $P<0.001$; Fig. 2), also with no significant difference between years ($\chi^2=0.0148$, df=1, $P>0.9$). In 1992 and 1993, the sex ratio was significantly more male-biased in the culled wing data than in the trap data (1992: $\chi^2=4.02$, df=1, $P<0.05$; 1993: $\chi^2=6.76$, df=1, $P<0.01$; Fig. 2).

The sex ratio (calculated from trap data) was significantly male-biased ($P<0.005$) on each night in 1992 and 1993 (except for one night in 1992 when the sex ratio was not significantly different from unity). There was significant heterogeneity in the sex ratio between nights (1992: $\chi^2=42.71$, df=11; 1993: $\chi^2=38.97$, df=11). In 1992 and 1993, the ratio of males to females within each moth family was significantly male-biased ($P<0.005$ for all families; Fig. 3). The sex ratio of moths trapped varied with moth family (1992: $\chi^2=11.04$, df=3, $P<0.001$; 1993: $\chi^2=43.92$, df=3, $P<0.001$).

The small sample sizes for the wing data precluded analysing those data by family or night.

Bat activity, as measured by both passes and buzzes, was significantly different across time periods (passes: $F_{2,190}=10.42$, $P<0.0001$; buzzes: $F_{2,190}=8.04$, $P<0.0005$; Fig. 4), with significantly higher activity (passes and buzzes) in the middle period of the night than in the early and late periods (Student–Neuman–Keuls test: $P<0.05$). The early and late periods were not significantly different. There were significant differences in activity levels between the two bat species for both passes ($F_{1,190}=9.64$, $P<0.002$; *L. borealis* > *L. cinereus*) and buzzes ($F_{1,190}=6.94$, $P<0.01$; *L. cinereus* > *L. borealis*). There was no significant interaction between bat species and period of the night for either passes or buzzes suggesting that...
patterns of activity over the night were similar for both *L. cinereus* and *L. borealis*.

In 1993, the ratio of males to females caught in the trap within each time period was significantly male-biased (early: 1.6:1, \( \chi^2 = 10.14, df = 1, P < 0.001 \); middle: 4.03:1, \( \chi^2 = 170.88, df = 1, P < 0.001 \); late: 3.06:1, \( \chi^2 = 30.51, df = 1, P < 0.001 \)). A comparison of mean moth density (number of moths/h) between periods of the night revealed a significant interaction between sex and period (\( F_{2,33} = 4.19, P < 0.03 \); Student–Neuman–Keuls test: \( P < 0.05 \); Fig. 5). Female activity decreased over the night but there were significant differences only between the early and late periods (\( F_{2,33} = 3.31, P < 0.01 \); Student Neuman–Keuls test: \( P < 0.05 \); Fig. 5). Similar patterns were observed in 1992, although activity was measured only in the early and middle periods that year; males were significantly more active in the middle of the night than early in the night (\( t = 2.89, df = 22, P < 0.01 \)), while females were significantly more active early in the night than in

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**Figure 3.** Number of male (□) and female (■) moths (expressed as percentage of total moths) from the families Noctuidae, Geometridae, Arctiidae and Notodontidae caught by a light trap in (a) 1992 and (b) 1993. Numbers above bars indicate sample sizes of moths captured.

**Figure 4.** Mean (+se) number of *L. cinereus* (□) and *L. borealis* (■) passes (a) and buzzes (b) per 10-min interval for early, middle and late periods of the night in 1993. Total number of 10-min sampling periods for each species was 48 in the early and late periods and 100 in the middle period. Activity was sampled 1 night a week for 12 weeks from early June to late August 1993.
Figure 5. Mean (+SE) number of male (□) and female (■) moths caught per h by a light trap in the early, middle and late periods of the night in 1993. Trap was set once a week for 12 weeks from early June to late August 1993.

the middle of the night (t=−1.94, df=22, P<0.04).

Because female *Lymantria dispar* (gypsy moths) do not fly, this species was not included in the above analyses. In 1992 and 1993, all of the *L. dispar* caught in the light trap were male (*N*=58 and *N*=208, respectively). Similarly, all of the *L. dispar* wings dropped by the bats in 1992 and 1993 were from male moths (*N*=7 and *N*=19, respectively).

**DISCUSSION**

Overall, bat captures of four families of macrolepidopteran moths were significantly male-biased, a pattern also observed in moths collected in light traps. The sex ratio of each family of moths caught in the trap was significantly male biased, but there were significant differences between families in the ratio of males to females. Captures in light traps indicated significant differences in the times of peak activity between male and female moths, with male activity peaking in the middle of the night and female activity peaking earlier in the night. Bat activity was significantly higher in the middle part of the night than in the early and late periods of the night.

Sexual dimorphism in the flight activity of moths is the most likely explanation for the male-biased predation I documented. Females may have been at a lower risk of bat predation because they flew less than males and did most of their flying at different times than males. Bat activity appeared to coincide with overall moth activity (which was dominated by male moth activity). The peak in male moth flight activity corresponded with the peak in bat activity in the middle of the night. By not elevating their activity during this time period, female moths reduced their risk of predation. Bat activity around the lights reflects the overall activity patterns of *L. cinereus* and *L. borealis* in my study area. Radio-tagged *L. cinereus* and *L. borealis* at Pinery arrive at the lights within 30 min of becoming active, and spend most of their nightly foraging time within 500 m of the lights (Hickey & Fenton 1990, Hickey 1993). The greater male-bias seen in the culled wing data than in the light trap data could be another indication of sexual dimorphism in moth flight activity; females attracted to street lights may eventually stop flying and land close to the lights, whereas males (because of their tendency to fly more) would continue to fly and have a higher risk of being eaten by foraging bats. Light trap data would not reflect this behaviour because moths attracted to the light usually fall into the trap and cannot escape.

Some species of moth may avoid foraging bats by flying when bats are less active as has been suggested for *Malacosoma americanum* (Lasiocampidae; Lewis et al. 1993). Bat activity levels may also have influenced the phenology of sound-producing arctiid moths (Fullard 1977). Sexual dimorphism in moth flight times is supported by a laboratory study of daily flight times of male and female moths (Edwards 1962); females were most active between sunset and midnight, males between midnight and sunrise. Similar patterns have been witnessed in the field (Williams 1935, 1939). Peaks in male activity probably represent an active search for females (Edwards 1962), while female activity peaks early in the night may reflect females actively searching for ‘calling’ sites.

The heterogeneity among moth families in the sex ratio of moths captured in the trap could indicate taxonomic variation in the relative amounts of flying done by males and females. Alternatively, the differences could reflect temporal variation (between nights) in the emergence of males and females within a species. In many
insects (including Lepidoptera) males emerge before females, a phenomenon termed protandry (Wiklund & Fagerström 1977). The extremely male-biased sex ratios seen in the trapped Notodontidae and Arctiidae could have resulted from the initial emergence (dominated by males) of a single species on one night.

It is unlikely that protandry could explain the overall sex-biased predation I observed because the culled wing data were collected on many nights spread across the summers of 2 years. Biased sex ratios following eclosion of both sexes are unusual among Lepidoptera (Wagner & Powell 1988), thus it is doubtful that the male-biased predation I witnessed was a reflection of a male-biased sex ratio in the entire moth community at this site. Although there are cases in which the population sex ratio of some moth species is skewed, either towards males or females (e.g. Wagner & Powell 1988), most studies show a sex ratio close to unity (e.g. Dahlsen et al. 1992) following eclosion of both sexes.

An alternative explanation for the sex-biased predation on moths in my study is that relative to female moths, males are more attracted to lights as light traps sometimes catch relatively more males than do other methods (e.g. Hamilton & Steiner 1939; Weissling & Knight 1994). Hsiao (1973) indicated that there is no difference between the flight behaviour and paths of male and female moths flying to lights. However, he did not discuss whether there are inter-sexual differences in the likelihood of initiating phototactic flight. A plausible explanation for the discrepancy between trapping methods is that light traps exaggerate a naturally occurring sex-bias in flying moths. Because of their attractive power over relatively long distances (relative to passive traps), light traps may be more likely to catch the already volant and stronger flying individuals (i.e. males). Even if lights do exaggerate a naturally occurring sex-bias, this phenomenon is interesting because street lights are a common feature of the urban and rural landscape. Some bat species in all parts of the world exploit the predictable insect concentrations around lights (e.g. Fullard 1989; Acharya & Fenton 1992; Rydell 1992).

The preferential light attraction hypothesis, however, does not explain male-biased predation on cockchafers, Melolontha melolontha (Coleoptera), by aerially hunting Rhinolophus ferrumiquinum (Chiroptera: Rhinolophidae; Jones 1990). Like moths, cockchafers use pheromones for intra-sexual communication. The males' search for females appeared to place the male cockchafers at a higher risk of bat predation than the more sedentary females. The bats observed by Jones (1990) foraged over dairy pasture and woodland, areas relatively free of light pollution. The most parsimonious explanation for the sex-biased predation observed is that it was a consequence of sexual dimorphism in flight activity.

Although female moths apparently have a lower risk of predation than males do from aerially hunting insectivorous bats, the females' sedentary behaviour should make them more vulnerable to bats that glean prey from surfaces. Most gleaning bats use prey-generated cues to locate their prey (e.g. Tuttle & Ryan 1981; Marimuthu & Neuweiler 1987; Anderson & Racey 1993). One would predict that the sex ratio of moths eaten by gleaning bats would be near unity, or perhaps even female-biased if female moths are more sedentary than males. There are no data available on the sex ratio of moths eaten by gleaning bats.

The flight dimorphism hypothesis predicts that bats hunting airborne prey will take only males in moth species where females are flightless. My data on Lymantria dispar, gypsy moths, support this prediction. Females of this species possess fully developed wings, but are practically flightless (Sattler 1991). I did not observe female L. dispar flying at Pinery, and the bats and light traps caught only males. Furthermore, in L. dispar there is sexual dimorphism in hearing (Cardone & Fullard 1988). Female L. dispar have significantly less sensitive ears in the 20–50 kHz range (sympatric bats echolocate at these frequencies) than do males. The females' best frequencies are in the 'non-bat' range of 10–20 kHz.

Apart from L. dispar, I found no data on sexual dimorphism in hearing in other species of moths. In mantids (Dictyoptera), however, auditory sexual dimorphism (females have reduced ultrasonic hearing) is common and closely tied to dimorphism in wing length (Yager 1990). Mantises with long (functional) wings have sensitive ultrasonic hearing while those with short (non-functional) wings do not. Predator avoidance has been suggested as a major function of hearing in many mantis species (Yager et al. 1990). If this hypothesis is true, then non-volant mantises would not need bat-detecting ears.
For night-flying insects in general, I predict that if there is sexual dimorphism in flight activity, then there will also be sexual dimorphism in predation risk from aerially hunting bats, and sexual dimorphism in auditory capability (for insects that hear ultrasound). Data from L. dispar support all of these predictions; however, in this species females do not fly. For species of moths where females fly (but less than males), data on possible sexual dimorphism in hearing are lacking. Where females fly (but less than males), data on possible sexual dimorphism in hearing are lacking. For mantids, there are data on sexual dimorphism in hearing, but none on predation risk from hunting bats. The results of this study provide field evidence of sex-biased predation on moths, and support the hypothesis that searching for mates is a risky behaviour.

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